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SELF-INCOMPATIBILITY MECHANISMS  
IN FLOWERING PLANTS:  
SOME COMPLICATIONS AND CLARIFICATIONS

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INTRODUCTION

It is curious fact that whereas modern Floras frequently aim to include additional biological information about plant species, such as chromosome number or ecological data, with very few exceptions breeding systems have been neglected. This situation is further evinced by the publications devoted to chromosome numbers (eg. FEDEROV, 1968; RAVEN, 1975) and the lists of additional and updated chromosome counts which regularly appear in *Taxon* under the auspices of the IOPB. Likewise, there are regularly published virtually encyclopaedic accounts of palynological data (eg. WALKER & DOYLE, 1975; NOWICKE & SKVARLA, 1979; LINDER & FERGUSON, 1985) for diverse families and genera. In contrast, there have been no equivalent attempts to monitor data on the breeding systems of flowering plants or even the occurrence of just one facet of this topic, the existence of self-incompatibility -with the exception of heteromorphic self-incompatibility (ie. heterostyly or diallelic SI) which has received two excellent review articles by VUILLEUMIER (1967) and GANDERS (1979). But in general we are still uncomfortably ignorant of the extent of occurrence of self-incompatibility mechanisms even at the level of the family.

Two examples may serve to illustrate this situation. Recent publications by LEVIN (1986) and RICHARDS (1986) each provide an estimate of the number of families with homomorphic, gametophytic self-incompatibility. LEVIN (*op.*

*cit.*, p. 218) claims that this mechanism occurs in 78 families, whilst RICHARDS (*op. cit.*, p. 195) reports that gametophytic SI is present in 71 families. Such relative precision and agreement between two authors implies that there is a firm data base available for these estimates but, unfortunately, this is not the case. LEVIN (1986) does not provide any references to support his estimate of 78 families but RICHARDS (1986) cites two sources, DARLINGTON & MATHER (1949) and BREWBAKER (1957). The former authors suggested that 'half of the species of angiosperms have self-incompatibility' but this seems to be little more than a guess-estimate based on no provided evidence. BREWBAKER (1957) derived his information primarily from two sources, EAST (1940) and FRYXELL (1957), and incidentally listed 66 families having taxa with self-incompatibility.

EAST (1940) is an excellent pioneer compilation of taxa reported to show self-sterility which is all the more impressive when one recalls that it was written at a time when many basic aspects of self-incompatibility systems were still unknown. For example, the nature and occurrence of homomorphic sporophytic self-incompatibility in the Compositae was reported a decade later by GERSTEL (1950) and HUGHES & BABCOCK (1950). That the same mechanism occurs in the Cruciferae was subsequently elucidated by BATEMAN (1954) and THOMPSON (1957). As a consequence, EAST (1940) is a useful and extensive survey but one which needs to be viewed from a historical perspective, particularly since it is based only in part on East's own observations, and otherwise on a mixture of variable and occasionally anecdotal sources. Not surprisingly there are a number of errors. The outstanding pioneer value of East's review is not in doubt. What is surprising is that it should be cited so frequently as a source on SI mechanisms nearly half a century later.

FRYXELL (1957) is a rather more rigorous work since each species reported as self-incompatible is provided with a reference, although again EAST (1940) is a primary source which is cited repeatedly. However, since FRYXELL (*op. cit.*) records only some 60 families with self-incompatible taxa, and this number also includes species with homomorphic, sporophytic and also heteromorphic SI, it is difficult to sustain the estimates of 78 or 71 families with gametophytic SI alone as reported by LEVIN (1986) and RICHARDS (1986).

The lack of information concerning the extent of occurrence of self-incompatibility in angiosperm families reflects a narrow data base at the species level. Basic texts which explain self-incompatibility usually discuss three kinds of mechanism: homomorphic, gametophytic (GSI), homomorp-

hic, sporophytic (SSI), and heteromorphic self-incompatibility (Het SI). See Figs. 1-3 for summary. It should be appreciated that these mechanisms are based on very few species which have been studied in detail either for the nature of the genetic control of SI, or for aspects of the cellular-molecular interactions which cause the inhibition of self pollen.

This situation has several consequences. Firstly, any generalisations concerning the evolution and functioning of SI mechanisms can at best only be considered to be very tentative. A more serious consequence is that the impression that SI mechanisms are well understood phenomena which is created by some basic texts may actually act as an obstacle to further studies, and furthermore, experimental observations which do not accord with those classical models may have been set aside. Two areas where an accumulation of dogmata has hindered our appreciation of the diversity of self-incompatibility phenomena, the nature of 'sporophytic' incompatibility, and cases where self-pollen seems to have an ovarian site of inhibition, are further considered below.

#### HOMOMORPHIC AND HETEROMORPHIC, 'SPOROPHYTIC' SELF-INCOMPATIBILITY

In common with some other authors (eg. NETTANCOURT, 1977) the recent work by LEVIN (1986) makes a major distinction between 'sporophytic' and 'gametophytic' self-incompatibility and although only the three families Compositae, Cruciferae and Convolvulaceae(\*) are initially listed under the former heading (LEVIN, *op. cit.* p. 218), it subsequently becomes evident that heteromorphic taxa are referred to the same general mechanism. GIBBS (1986) has argued that the grouping of homomorphic (multiallelic) sporophytic SI and heteromorphic (diallelic) SI is unsupported by any evidence and is therefore misleading. Only the following points need to be reiterated here.

(a) Homomorphic, sporophytic SI is only known to occur with certainty in two families, the Compositae (GERSTEL, 1980; HUGHES & BABCOCK, 1980; CROWE, 1954); and Cruciferae (BATEMAN, 1954, 1956; THOMPSON, 1957), and possibly also the Betulaceae (THOMPSON, 1979; ME & RADICATTI, 1983). Heteromorphic SI is widely scattered, sometimes in isolated genera, in some 24 families (GANDERS, 1979).

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(\*) There does not seem to be any experimental evidence to warrant inclusion of the Convolvulaceae as a family with homomorphic, sporophytic SI.

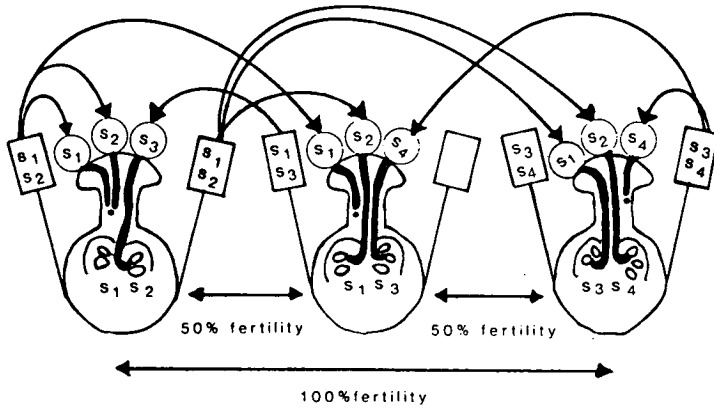


Fig. 1. Homomorphic, gametophytic SI. In the classic mechanism genetic control is by means of a single locus  $S$  with a series of alleles in the population. Each allele,  $s_1, s_2, s_3, \dots$  acts independently and (self) incompatibility occurs when products of the  $s$  allele in the pollen tube encounter products of the same  $s$  allele in the stylar transmitting tissue. In some taxa there is polyfactorial control with two (Gramineae) or rarely more (*Ranuncunculus acris*, *Beta vulgaris*) multiallelic SI loci.

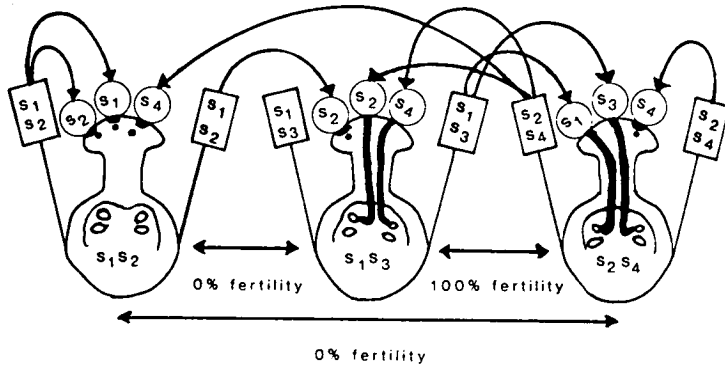


Fig. 2. Homomorphic, sporophytic SI. Genetic control is also determined by a single locus  $S$  with multiple alleles in the population. Each haploid pollen grain, although clearly bearing only one  $s$  allele in its nucleus, carries the incompatibility reaction of *both*  $s$  alleles present in the pollen parent. As a consequence note that pollen grains with the  $s_2$  allele derived from a  $s_1 s_2$  plant are incompatible on a  $s_1 s_3$  stigma whereas  $s_2$ -bearing pollen grains from a  $s_2 s_4$  pollen parent are compatible on  $s_1 s_3$  stigmas. Hierarchical dominance-recessive reactions may exist between  $s$  alleles in the pollen or stigma which, for simplicity, are omitted in Fig. 2.

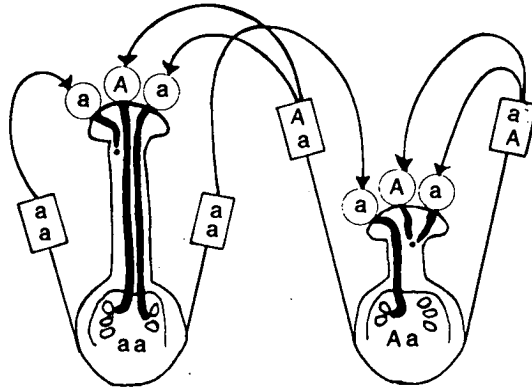


Fig. 3, Heteromorphic SI. Simplistically, genetic control is determined by one locus (A) with two alleles, one dominant, A and one recessive, a. The mechanism is associated with floral dimorphy, commonly but by no means always, including heterostyly. In *Primula* spp. long-styled morphs are homozygous recessives, aa, and short-style morphs are heterozygotes, Aa. The system functions by a sporophytic mechanism in the sense that all the pollen grains and also the stigma/stylar tissues of the heterozygotes function phenotypically with the incompatibility reaction of the dominant allele. Consequently, compatible pollinations are effectively: a x A and A x a. In fact, rather than a single locus, genetic control is heteroallelic with a 'supergene' or tightly clustered series of loci with dominant or recessive alleles which determine not only the SI reaction but also the facets of the floral architecture - style length, anther level, pollen size, etc.

(b) In taxa with homomorphic, sporophytic SI the incompatibility reaction always takes place at the stigmatic surface. Incompatible pollen is either incapable of rehydration and germination or the pollen tube is unable to penetrate the stigmatic papillae. Commonly, a localised callose deposition occurs in papilla cells adjacent to the SI pollen or pollen tube (DICKINSON & LEWIS, 1973).

Various studies have implicated proteins located in the pollen-wall in this incompatibility reaction (HESLOP-HARRISON & al., 1974), most strikingly in the mentor effect with *Cosmos bipinnatus* (HOWLETT & al., 1975). In this experiment, an extract of pollen-wall proteins derived from compatible ('cross') pollen mixed with live incompatible self-pollen caused the latter to break the self-incompatibility mechanism. It is probably significant that whereas the proteins encapsulated in the pollen intine wall layer are derived from the haploid gametophytic cell, the proteins of the exine cavities are

derived from the breakdown residues of the tapetum and so are of sporophytic origin (HESLOP-HARRISON & al., 1973). Confirmation of the role of such pollen wall-held proteins by way of isolation of s-allele linked fractions from pollen extracts is as yet lacking, but there is good evidence for the presence of such s-allele linked glycoproteins in the stigma (NISHIO & HANATA, 1982).

None of these circumstances applies to taxa with heteromorphic (sporophytic) SI. In contrast to the incompatibility reaction in species with SSI, the blockage to self pollen tubes does not occur uniformly at the stigmatic surface in Het SI. Rather, penetration of the stigma is not uncommon and quite extensive pollen tube growth in the style may take place (BAWA & BEACH, 1983; SCHOU & PHILIPP, 1984). Differential self pollen tube growth in long-style versus short-style floral morphs is also found in a number of species (LEWIS, 1943; SCHOU, 1984). Likewise, there is no evidence for the involvement of pollen wall-held proteins (ie. mentor type effects or consistent callose reaction at the stigma) in Het SI species, and attempts to isolate s-allele linked proteins from stylar extracts have also proved unsuccessful with such taxa (see GIBBS, 1986 for review).

There is thus little justification on present evidence to group homomorphic, sporophytic and heteromorphic, sporophytic SI mechanisms together. On the contrary, the scattered (taxonomic) distribution of Het SI indicates that this type of system most likely evolved repeatedly and independently, and consequently may include rather different pollen tube inhibition mechanisms.

## LATE ACTING SELF-INCOMPATIBILITY

In most examples of homomorphic, gametophytic SI the growth of incompatible pollen tubes is arrested in the stylar transmitting tissue, sometimes with swelling or bursting of the tip. However, an increasing number of examples have accumulated in the literature which report that the incompatible pollen tubes are not inhibited before they reach the ovary where they may actually penetrate the ovules.

*Theobroma cacao* -Sterculiaceae (KNIGHT & ROGERS, 1955; COPE, 1962), has been traditionally cited as the sole example of this phenomenon but there are several other early studies from diverse families, ef. *Gasteria verrucosa* Liliaceae (SEARS, 1937), *Medicago sativa* - Leguminosae (BRINK & COOPER, 1939), *Lotus corniculatus* -Leguminosae (BUBAR, 1959), and an increasing number of more recently described cases, eg. *Sterculia chicha* - Sterculiaceae

(TARODA & GIBBS, 1982), *Acacia retinodes* - Leguminosae (KENRICK & al., 1984). We have also encountered a similar situation in *Ceiba* species - Bombacaceae (GIBBS, SEMIR & CRUZ, unpublished studies), and *Tabebuia caraiba*, and *T. ochracea* - Bignoniaceae (GIBBS & BARROS, unpublished studies). Nor is ovarian incompatibility limited to homomorphic taxa, since it also seems to occur in heterostylous species such as *Anchusa officinalis* (SCHOU & PHILIPP, 1984) and various Rubiaceae, eg. *Warszewiczia coccinea* (BAWA & BEACH, 1983). SEAVEY & BAWA (1986) have referred to this general phenomenon as 'late-acting self-incompatibility' in a recent review paper in which they cite some 25 examples.

In the classic example of *Theobroma cacao* KNIGHT & ROGERS (1955) and COPE (1962) reported discharge of the male gametes into the embryo sac but failure of syngamy. Ovaries with a critical number of non-fusion ovules failed to develop fruits. In *Acacia retinodes* KENRICK & al. (1984) suggest that self pollen tube inhibition occurs in the nucellus and syngamy does not occur. However, in *Asclepias syriaca* both syngamy and endosperm nucleus formation are reported, but only the endosperm nucleus begins to divide and early abortion follows (SPARROW & PEARSON, 1948). Syngamy is also reported in *Lotus corniculatus* (BUBAR, 1959).

Clearly, some of these cases of ovarian self-incompatibility intergrade with other situations where self-incompatibility has not been established but in which differential seed-set occurs following self- versus cross-pollinations, eg. *Fagus sylvatica* - Fagaceae (BLINKENBERG & al., 1958), *Lotus jacobeus* and *L. tenuis* - Leguminosae, (BUBAR, 1958), and the interesting case of *Borago officinalis* (CROWE, 1971) in which a polygenic 'feed-back' type of mechanism causes increasing self-sterility in the progeny of initially self-fertile plants.

Unfortunately, in most species which appear to have late-acting self-incompatibility we simply do not know what happens after self-pollen tubes reach the ovary and detailed histological studies, either with sectioned material or cleared ovules, are urgently required for such taxa. It seems certain that 'late-acting SI' covers a range of situations including some pre-zygotic mechanisms, ie. SI in a strict sense, and others involving post-zygotic events. Some of the former may simply represent examples of species with essentially GSI (eg. *Acacia retinodes* ?) or Het SI (eg. *Anchusa officinalis*) but with a delayed incompatibility response. Other cases may represent a novel gamete-gamete level of SI reaction. The post-zygotic situations involving embryo abortion may likewise represent a novel form of SI mechanism or, perhaps more likely, comprise a whole range of self-sterility phenomena with rather generalised genetic control. At present we simply do not know

enough about the nature or control of the threshold or 'trigger' events which lead to selfed ovule abortion.

These examples of 'late-acting SI' also seem to overlap with current ideas on 'sexual selection' or 'female choice' (WILLSON, 1979; STEPHENSON & BERTIN, 1983), although this is a general area where theory tends to outstrip empirical evidence. Certainly a few studies, eg. STEPHENSON & WINSOR (1986) have produced good evidence for the occurrence of 'female choice' in *Lotus corniculatus*. These authors were able to show that seed of surviving fruits in plants which had naturally self-thinned fruit set were fitter (as assessed by comparison of vegetative growth and reproductive output of progeny) than such seed of plants subjected to random hand-thinning. However, other studies (WIENS & al., 1987) indicate that embryo abortion can have a simple mechanistic cause due to competition, eg. for hormonal stimuli, between young fruits with few versus many developing seeds. In any case, it should be emphasised that these examples of embryo abortion report events in cross-pollinated rather than selfed flowers.

## CONCLUSIONS

The traditional textbook view that most hermaphrodite flowering plant species can probably be referred to one or other of three relatively clear-cut self-incompatibility mechanisms -GSI, SSI or Het SI- is now very difficult to sustain, and it is evident that SI systems are much more diverse and complex than previously thought to be the case. Phenomena which have been hitherto considered to be rather exceptional, such as cryptic self-incompatibility (BATEMAN, 1956) or the polygenic control of outbreeding (CROWE, 1971), together with other poorly understood mechanisms such as 'late-acting SI' may be quite widespread.

Two examples may serve to illustrate this point. In a recent study, BOWMAN (1987) has demonstrated the existence of cryptic self-incompatibility in *Clarkia unguiculata* -Onagraceae, of a genus previously considered to comprise self-compatible species. As BOWMAN (*op. cit.*) points out, this mechanism would not normally be detected by standard experimental procedures in which seed set following selfing is taken as evidence of 'self-compatibility'. Certainly, *C. unguiculata* is not self-incompatible in a strict sense, but presumably differential self- versus cross-pollen tube growth ensures cross-fertilisations when mixed pollen loads are available. Another species previously considered to be self-compatible on the basis of earlier



studies is *Vaccinium corymbosum* -Ericaceae. In this case, VANDER KLOET & LYRENE (1987) have convincingly shown the presence of distinct self-incompatibility with very poor seed-set (but with fruit-formation) following self-pollination. Similar, rather cryptic SI mechanisms may operate in other taxa of this family, eg. *Kalmia* species (JAYNES, 1968) and some *Rhododendron* species (WILLIAMS & al., 1984). Interestingly, in this latter study the authors report 'late acting SI' and early embryo abortion. We do not know as yet whether these SI phenomena in the Ericaceae represent a common mechanism and if so whether this has the same genetic control as classical GSI.

With regard to possible polygenic systems it is of interest that MULCAHY & MULCAHY (1983) have suggested a model for a complementary gene action type of system in which SI is an expression of genetic load. Rather unfortunately, these authors chose to present their hypothesis as a direct challenge to the occurrence of one locus, multiallelic GSI, but as LAWRENCE & al., (1985) have lucidly counter-argued, there is good evidence for classical GSI in many taxa. Nevertheless, given some of the diverse post-pollination phenomena which occur, it is possible that a polygenic type system may operate in other taxa which lack GSI.

This leads to a final, admittedly very speculative, point. Perhaps our general view of SI mechanisms in flowering plants has been misconceived. There has been a tendency to consider that GSI is a particularly widespread mechanism which is present in many families, but which just happens to be exemplified by the relatively few, well studied 'classic' examples, eg. *Trifolium repens* (Leguminosae), *Lilium longiflorum* (Liliaceae), *Oenothera organensis* (Onagraceae), *Papaver rhoeas* (Papaveraceae), *Petunia hybrida*, *Nicotiana glauca* (Solanaceae), *Prunus avium* (Rosaceae), etc. However, it is possible that these examples might actually represent the majority of taxa with GSI, and that many angiosperm groups have other, rather different, poorly explored SI mechanisms.

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